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PROTANDRIC HERMAPHRODITISM IN A MOLE CRAB, *EMERITA ASIATICA* (DECAPODA:ANOMURA)

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Abstract

Protandric hermaphroditism in a mole crab, *Emerita asiatica*, is described. Neotenous males occur at 3.5 mm carapace length (CL) and above, whereas females acquire sexual maturity at 19 mm CL. The neotenous males, as they continue to grow, gradually lose male functions and reverse sex around 19 mm CL. The disappearance of genital papillae is the first visible sign of sex reversal; spermatogonial activity in testes ceases but hyperactivity of the mesodermic cells ensues. In the CL range of 19–22 mm, the male's gonad comprises inactive testicular and active ovarian portions; the median ovarian limb beyond the fused posterior extremity of the testes lacks testicular elements; and the vas deferens is intact but a pair of functional oviducts is formed. These intersexuals possess three pairs of pleopods. A few have eggs, and thus constitute secondary females in the population. Androgenic glands, active in the neotenous males, show signs of degeneration in the larger males, and disappear in the intersexuals. The mesodermic cells of the gonad undergo important functional changes during sex reversal. Sex-changers with incomplete transformation of testis into ovary and imperfectly differentiated oviducts are also reported.

Introduction

In mammals the histogenesis of the gonad as an ovary or testis is determined by the sex genes that initiate chemical synthesis of substances responsible for sexual differentiation (Witschi, 1971). The malacostracan crustaceans are generally gonochoristic with genetically determined sex. But several of them exhibit both functional and non-functional hermaphroditism. Functional protandric hermaphroditism has been well documented in the deep-sea prawns and two isopod groups, *Cymathoides* and *Cryptoniscidae* (Yaldwyn, 1966; Charniaux-Cotton, 1975a). Here, each sex possesses complete genetic information for the morphogenesis of both sexes. The genes for male morphogenesis act in the presence of an androgenic gland hormone and for females in its absence (Charniaux-Cotton, 1960a).

Other groups of crustaceans may well show change of sex with growth, but evidence is rather meager. Mole crabs, including various species of *Emerita*, are typical burrowing forms on the wave-washed sandy beaches of temperate and tropical seas. Several species show sexual dimorphism in size. For example, the males of *E. asiatica* acquire sexual maturity soon after their metamorphosis from megalopa larvae (3.5 mm carapace length, CL) while the females attain it after considerable growth (19–22 mm CL) (Subramoniam, 1977). This size distinction at sexual maturity of *Emerita* is considered a characteristic feature of the genus by Efford (1967). Barnes and Wenner (1968), on the contrary, proposed a protandric hermaphroditism based on sex-ratio studies on *E. analoga*. However, the sex ratio

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Abbreviations: CL, carapace length.

studies of Wenner (1972) failed to strengthen the likelihood of a sex reversal in *E. asiatica*, the overlap in size range between males and females being too wide to suggest sex reversal (Subramoniam, 1977). The neotenic males grow up to 11 mm CL without reduction in size of the gonadal apparatus. Judging from the linear increase of the male gonadal apparatus with general body growth, Subramoniam believed that the neotenic males of *E. asiatica* do not change sex as they grow.

The present paper dealing with *E. asiatica* reports new data on the continued growth of larger males, which pass through an intersexual phase before some obtain complete functional protandric hermaphroditism.

Materials and Methods

Specimens of *Emerita asiatica* Milne Edwards, belonging to the family Hippidae (Decapoda:Anomura), were collected from the intertidal regions of the Marina beach, opposite the Madras University buildings, Madras, India. This crab has distinctly zoned habitats in the intertidal region, the smallest individuals being commonest in the fine sand near the high water mark and the largest in coarse sand near the low water mark. Between these two zones, specimens of intermediate sizes are found (Alikunhi, 1944; Subramoniam, 1979a). At least 60 crabs 3.5–33 mm CL were hand-picked every fortnight and brought to the laboratory.

Male and female *Emerita* specimens were distinguished following the descriptions given by Subramoniam (1977). Genital papillae at the base of the coxae of the fifth thoracic leg identified males. The females were recognized by the occurrence of three pairs of ovigerous pleopods in the abdomen. Specimens of both the sexes were dissected to observe the developmental stages of reproductive organs. For histological studies, the gonad was fixed in Bouin's and neutral formaldehyde. Paraffin sections were cut 6 μm thick and stained in haematoxylin and eosin.

Results

Reproductive structures of primary females and males

In females, the ovary is a paired organ lying partly in the thorax and partly in the abdomen. The anterior ends of the ripe ovary consist of two lobes each, one extending forward and the other to the side. The posterior parts of the paired ovary are connected by a transverse bridge of ovarian tissue lying over the pyloric region of the stomach. Behind the posterior paired parts, the ovary is fused to form a median cord which extends to the fifth abdominal segment (Fig. 1a). A pair of oviducts take their origin from the middle region of the paired posterior limb and open at the base of the coxae of the third thoracic leg. Externally, there are three pairs of pleopods in the ventral region of the first three abdominal segments.

In males too, the testis is paired but fused at the posterior extremity, a region corresponding to the posterior fusion of the ovarian limbs. The prominent vasa deferentia originate from the region where the limbs of the testes fuse (Fig. 1b) and open into the genital papillae at the base of the coxae of the fifth thoracic leg. There are no pleopods in the abdominal segments.

In neotenous males the testis is composed of several acini. The spermatogonial cells border the wall of the acinus while the spermatocytes and developing spermatozoa occupy the lumen. But these are so crowded in the active stage that the regular acinar arrangement is not often clearly demarcated (Fig. 2). Non-germinal somatic mesodermal cells are rare, and are found only between the closely packed

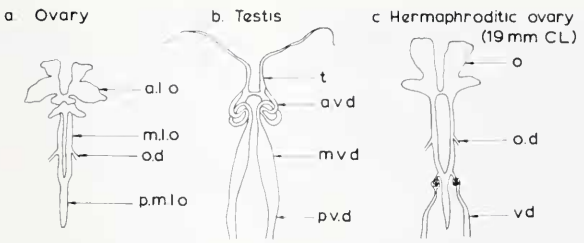

FIGURE 1. Diagrammatic representation of the testis, ovary, and the hermaphroditic ovary. t = testis; a.v.d. = anterior vas deferens; m.v.d. = mid vas deferens; p.v.d. = posterior vas deferens; a.l.o. = anterior ovarian lobe; m.l.o. = middle ovarian lobe; o.d. = oviduct; p.m.l.o. = posterior median ovarian limb; o = ovary; v.d. = vas deferens.

acini. In primary females—crabs that are female at the outset—the pleopods begin to appear at an early stage, ±12 mm CL (Subramoniam, 1977). Similarly, a pair of female gonopores appears at ±10 mm CL in primary females, whereas in the secondary females, originally males, they appear at ±19 mm CL.

Gonadal changes during sex reversal

Contrary to earlier observations (Subramoniam, 1977), males above 11 mm CL have been recorded. In them, the genital papillae gradually become smaller. The testes and vas deferens are intact and do not regress in size. However, histological sections of the testis of a 15 mm CL male whose genital papilla is completely reduced show remarkable changes in the cellular organization (Fig. 3). Testicular acini lined with spermatogonial cells are confined to a few places, and they do not contain spermatocytes and spermatids. As the testis loses its function, the somatic mesodermal cells become hyperactive and multiply to occupy the whole space made available by the shrinking testicular acini. These cells increase in size. They contain a large quantity of acid muco-polysaccharides as determined by histochemical tests. The vas deferens contains the spermatozoa and the spermatophoric ribbon. There is no evidence for any oocyte differentiation in the testis.

Though testicular activity ceases completely around 15 mm CL, sex reversal appears to occur only in the size range 19–22 mm CL. Although sex-reversed crabs resemble females externally (genital papillae absent; pleopods well formed and sometimes with eggs), they possess a hermaphroditic ovary with testicular portions intact. Curiously enough, in one such crab, measuring 19 mm CL, the paired testis portion was white, but along its mid-dorsal line were strings of golden-yellow oocytes. The posterior median cord is always yellow. A cross section through the testicular limb shows that it comprises two well-defined portions: the testicular acini and an ovarian region enclosing a central cluster of oogonial cells surrounded by oocytes in generative, post-pachytene, previtellogenic, and yolk-laden vitellogenic phases (Fig. 4). The germinal zone of the ovary contains very actively dividing oogonial cells, and the primary oocytes surrounding the germinal zone show features of early prophase of the first meiotic division (Fig. 5). By contrast, the testicular acini have no spermatocytes in the lumen, nor do the spermatogonial cells bordering the acini show any sign of activity. The nuclei of these resting spermatogonial cells contain clumps of chromatin. However, some of these cells are enlarged, with basophilic cytoplasm characteristic of primary oocytes in the premeiotic stage (Fig. 6). Mesodermic cells are not found in the testicular portion, but are seen in large

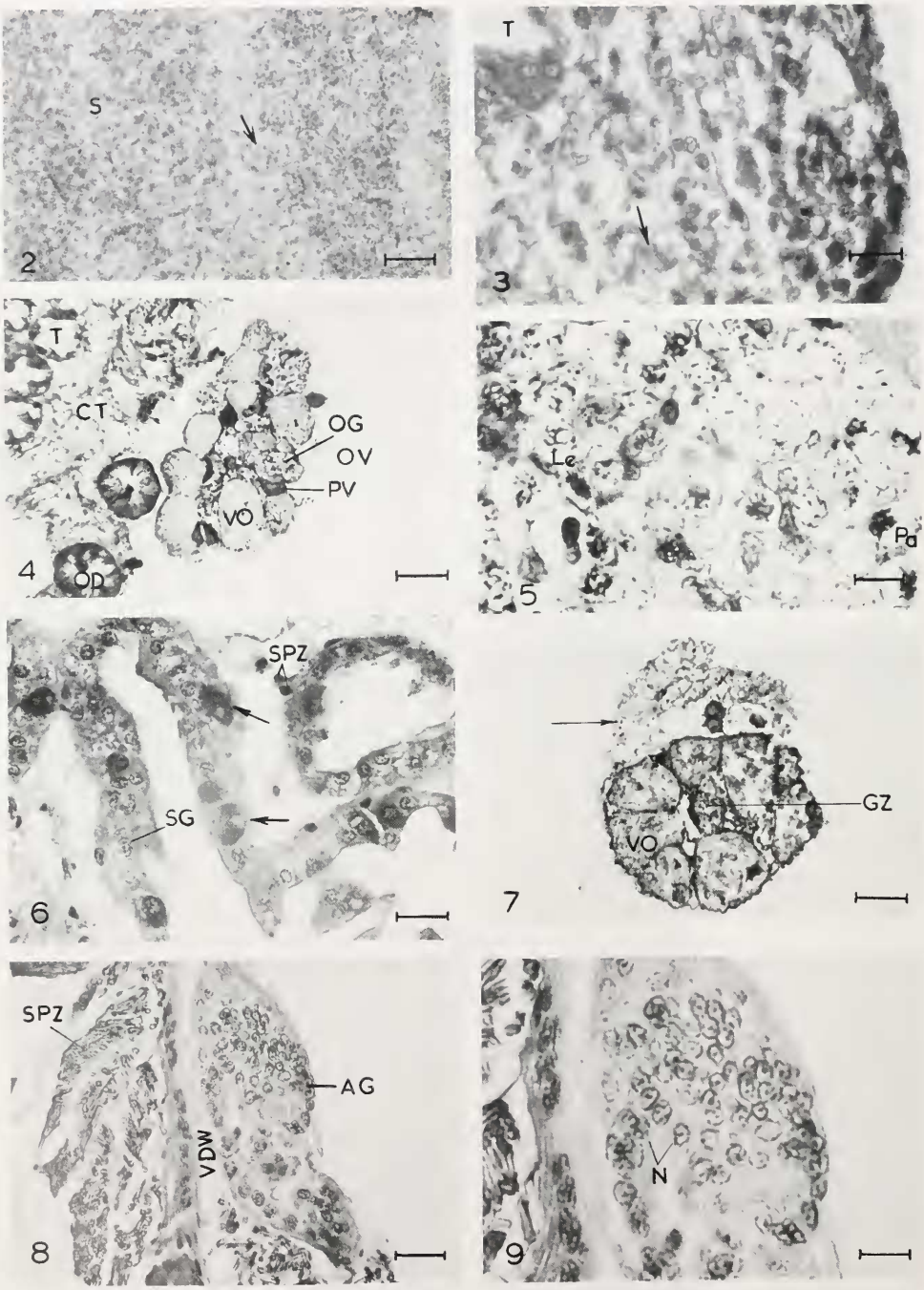

FIGURE 2. Section through the testis of an active male (5 mm CL) showing the closely packed acini (arrow) with developing spermatozoa (s) in them. Bar = 20 μm.

FIGURE 3. Transverse section through testis of a large male (CL 15 mm) indicating hypertrophy of the somatic mesodermal cells (arrows). T = testicular acinis. Bar = 20 μm.

FIGURE 4. Section of a hermaphroditic ovary of *Emerita asiatica* (19 mm CL). The testicular acini (T) contain spermatogonial cells, the lumen is devoid of spermatocytes and spermatozoa. The

numbers in the ovarian region; the vitellogenic oocytes are, in fact, surrounded by them. Pockets of primary gonial cells have also been observed in the testicular region.

The median posterior limb of the ovary is devoid of testicular elements but possesses a basal germinal zone with previtellogenic and vitellogenic oocytes arranged centripetally. The median ovarian cord at the point of its origin contains the basal laminar tissues without any testicular portion attached (Fig. 7) although the more posterior part of this ovarian limb contains only ovarian cells. In several such hermaphroditic females the vas deferens was intact and contained spermatophores, although the genital papillae through which the vas deferens opens were completely sealed off. A pair of functional oviducts formed anterior to the vas deferens had openings on the base of the third walking legs. Sixteen specimens of such intersex crabs were obtained in October–November 1978 in the size range of 19–22 mm CL. Similar forms were also obtained in subsequent collections. The occurrence of such secondary females was recorded earlier in a population of *Pandalus borealis* (Carlisle, 1959).

Androgenic gland and changes in functional morphology during sex reversal

The androgenic gland of *Emerita* has not been previously described. In reproductively active males (± 5 mm CL) it is simple cellular strands, as in brachyuran crabs such as *Carcinus maenas* (Charniaux-Cotton *et al.*, 1966). These strands lie in the subterminal portion of the distal vas deferens. The gland is composed of compactly packed columnar cells (Fig. 8), whose nuclei are ovoid, conspicuous, and endowed with dense chromatin (Fig. 9). Dense secretory materials with vacuoles of varying sizes fill the cytoplasm. The lobes of the androgenic gland are either spread out on the distal regions of the vas deferens or hang freely in the haemocoel with their bases attached to the outer layer of the vas deferens.

By contrast, the androgenic glands of a larger male (CL 9 mm) show many degenerative changes (Fig. 10). The majority of the glands have degenerated and a fine granular central portion without evidence of the normal cellular structure is evident. On one side are many pycnotic nuclei without any trace of cell walls, suggesting recent disintegration of cells (Fig. 11). However, new cordons of cells proliferate on the periphery of the gland, mostly in the basal region with which it is attached to the vas deferens wall. The cells of the new cordons are smaller than those of the androgenic gland of neotenic males. The degenerative areas of the

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ovarian part (OV) is separated by strands of connective tissue (CT). The oogonial cells (OG) are in the center surrounded by previtellogenic (PV) and vitellogenic (VO) oocytes. OD = Oviduct. Bar = 100 μm.

FIGURE 5. Higher magnification of germinal zone. Nuclei of many oocytes in the generative phase show thread-like chromosomes believed to represent leptotene (Le) and pachytene (Pa) stages. Bar = 10 μm.

FIGURE 6. Testicular acini showing oocytes in previtellogenesis (arrow). Note the basophilic cytoplasm of the previtellogenic oocytes. Spermatogonial cells (SG) are in the resting stage. Follicular cells are absent and a few residual spermatozoa (SPZ) are present. Bar = 25 μm.

FIGURE 7. Cross section through the proximal region of posterior median cord of the ovary. Germinal zone in the centre (GZ) surrounded by vitellogenic oocytes (VO). The connective tissue basal lamina contain many follicle cells (arrow). Bar = 100 μm.

FIGURE 8. Transverse section through the androgenic gland of a neotenous male (5 mm CL) AG = androgenic gland; VDW = vas deferens wall; SPZ = spermatozoa. Bar = 30 μm.

FIGURE 9. Higher magnification of the androgenic gland. Note the hyperactive nuclei (N) with dense basophilic material clumping on the nuclear wall. Bar = 13 μm.

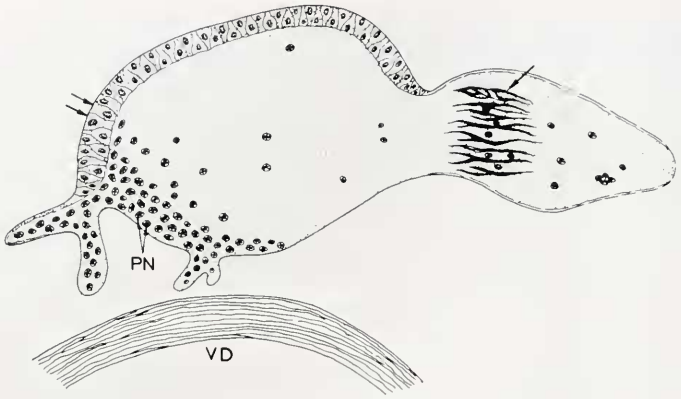


FIGURE 10. Composite diagram of androgenic gland of a large non-functional male (CL 9 mm). Large portion of the gland shows cellular degeneration (stippling). Scar-like thickenings (single arrow) are evident in the distal region of the gland. New cordon of cells appears in the basal region (double arrow). Figure not drawn to scale. V.D. = vas deferens; P.N. = pycnotic nuclei.

gland conform to the descriptions by Charniaux-Cotton (1960b, 1962) and Payen (1972). At the distal end of the gland are scar-like thickenings (Fig. 10). This region is devoid of regenerating cordons of cells; pycnotic nuclei have wheel-shaped chromatin clumps adhering to the nuclear membranes. At 15 mm CL and above, the androgenic gland was not detected.

Observation on incomplete sex reversal

Sexual reversal is not always complete; in some forms the males fail to become functional secondary females and remain intersexual. Two large crabs (CL 28, 29 mm) with well developed female secondary sexual characters (three pairs of pleopods and a pair of gonopores on the coxae of the third leg) had hermaphroditic ovaries, which were white and very thick. Interestingly, the vas deferens is retained in such crabs although the genital papillae are absent. Histological examination of the ovary revealed that the sex reversal in these crabs was incomplete in that the separate ovarian portion never formed. The anterior half of the paired tubular gonad was dominated by oocytic differentiation whereas the posterior half possessed inactive testicular tissues. Sections of the anterior region of the gonad show vitellogenic oocytes arranged on the dorsal periphery of the testis (Fig. 12). Deeper, below the vitellogenic oocytes, lie the previtellogenic oocytes. The follicle cells surrounding the previtellogenic oocytes are very active. However, the vitellogenic oocytes are invaded by enlarged follicle cells (Fig. 12) involved in resorption of yolk products. That this process of yolk absorption is by way of enzymatic conversion is shown by the staining reactions of the yolk globules and the contents of the follicle cells inside the ooplasm. The yolk contents are eosinophilic whereas the corresponding granules in the follicle cells are basophilic. This suggests that the yolk products are dissolved by some hydrolytic enzyme released from the follicle cells dissolves the yolk products, engulfing them intact and storing them. Delamination of follicle cells into yolk-laden oocytes can also be seen occasionally (Fig. 13). The testicular region contains several acini, each lined by inactive spermatogonial cells. The lumen is also empty of differentiated gametes. The follicle cells in the anterior ovarian region are of normal size and shape, whereas those in the

testicular region are hyperactive (Fig. 14). A transverse section through the oviduct (Fig. 15) originating from the ovarian region shows that its differentiation is incomplete in that it does not acquire a lumen and remains as strands of tissues. This condition is in contrast to the well differentiated functional oviduct of the secondary female (Fig. 4). The gonadal composition described so far gradually changes towards the posterior region. Here, no vitellogenic oocytes are found and the number of previtellogenic oocytes is also limited. Much of the gonadal portion is occupied by the testicular acini, which in several regions are filled with mucous secretions (Fig. 16). Such mucus secretions are also found on the periphery of the gonad (Fig. 17). The proximal vas deferens originating from the posterior region of the gonad is intact and its lumen contains residual sperm cells mixed with luminal secretions (Fig. 17). Neither spermatocytes nor spermatozoa, however, are found in the gonad.

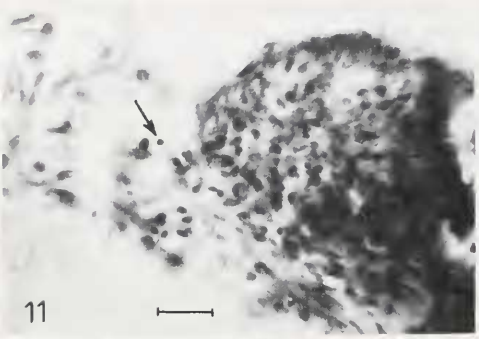
Discussion

It is evident from the table listing the size ranges of mature male and female of different species of *Emerita* that precocious sexual maturity of males, leading to neoteny, is widespread. However, the neotenous males tend to grow to larger sizes (Table 1). Size-related sex ratio curves in a well studied species, *E. analoga*, have led to the proposition of sex reversal (Barnes and Wenner, 1968; Wenner, 1972). Similar sex-ratio studies on *E. asiatica* males and females of different sizes, including an analysis of post-larval juveniles, do not support the contention of sex reversal (Subramoniam, 1977). Subramoniam suggested that the prevalence of males in the smaller size classes only indicated different growth rates between males and females, and that the absence of males in the larger size classes was due to mortality. More recently, Haley (1979) came to a similar conclusion from evidence he obtained that males of smaller size classes molt less frequently than females of the corresponding size in a hippid mole crab, *Hippa pacifica.*

The histological results reported in the present study demonstrate unequivocally the existence of functional protandric hermaphroditism in *Emerita asiatica.* Sex reversal in this crab is briefly reported elsewhere (Subramoniam, 1979b). The main reproductive events enumerated in Figure 18 indicate that neotenous males continue to grow after serving a normal male life (Subramoniam, 1977), deviate from normal sexual behaviour (Subramoniam, 1979c), gradually lose their secondary and primary sexual characters, and undergo sexual reversal by acquiring female characters at ± 19 mm CL. As a result of this, the population consists of two kinds of females: primary and secondary. Interestingly, the sex reversal of males into females occurs at the same size-range as sexual maturity of the primary females, which do not pass through a male phase (Fig. 18). Such a pattern of sexuality in the life history of *E. asiatica* has great adaptive significance by vastly augmenting the capacity to reproduce and to colonize the turbulent sandy intertidal zone. The precocious maturation of males that results in neoteny facilitates mating in the intertidal region without disturbing the normal activity of the females. Sex reversal, as exemplified by protandric hermaphroditism, increases the number of egg-laying females by adding secondary females to the female population.

Although environmental conditions may encourage the reproductive strategy, it is physical ease of sex reversal that lets it occur so frequently in malacostracean crustaceans.

The location of the germinal zone in the hermaphroditic crustaceans has long been debated. It is described either as the cortical germinal epithelial layer (*P. platyceros*, Hoffman, 1972) or as a single germinal zone at the basal lamella (*P. borealis* and *Lysmata seticaudata*; Charniaux-Cotton, 1975a). The hermaphroditic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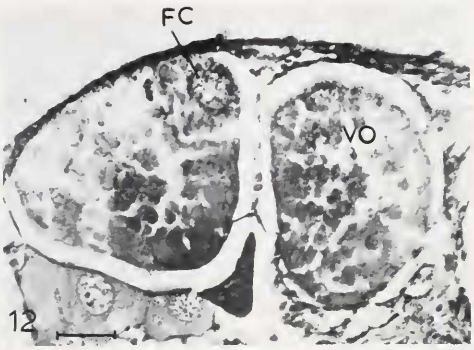
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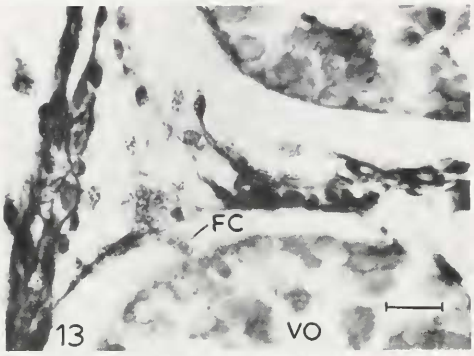
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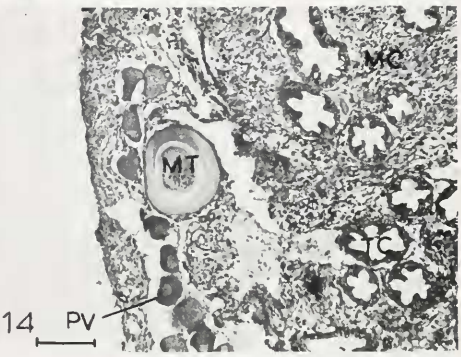
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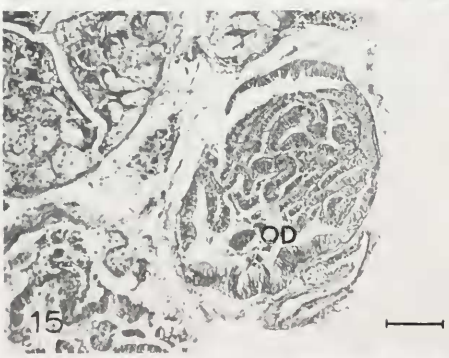
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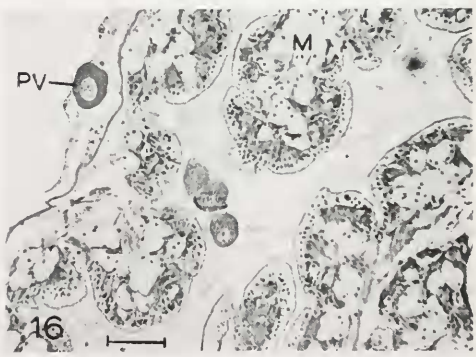
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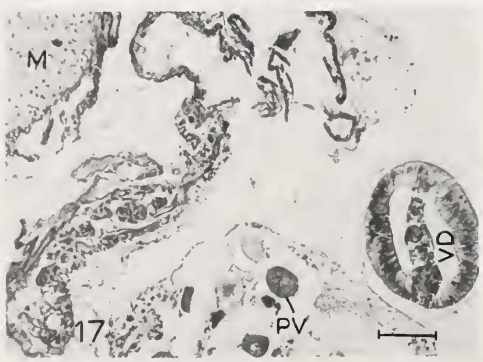
M
VD
17
PV

TABLE 1

Stage of sexual maturity of male and female Emerita *species.*

Species	Reference	Carapace length range of mature *Emerita* in mm	
		Male	Female
E. analoga	Knox and Boolootian, 1963	10.0–22.0	15.0–30.0
E. analoga	Efford, 1967	6.0–12.0	13.0–31.0
E. analoga	Barnes and Wenner, 1968	6.0–11.0	8.0–22.0
E. asiatica	Menon, 1933	3.5–7.5	22.0–30.0
E. asiatica	Subramoniam, 1977 and present study	3.5–15.0	19.0–33.0
E. austroafricana	Barnard, 1950	*–35.0	23.0–37.0
E. holthuisi	Sankolli, 1965	11.0–17.0	12.0–18.0
E. holthuisi	Achuthankutty and Wafar, 1976	*–10.0	10.0–15.3
E. portoricensis	Goodbody, 1965	*–8.0	9.0–17.0
E. rathbunae	Efford, 1967	2.5–**	33.0–41.0
E. talpoida	Wharton, 1942	3.8–14.0	*–26.0
E. talpoida	Efford, 1967	2.5–12.0	14.0–29.0

* Minimum size not given.
** Maximum size not given.

ovary of *E. asiatica* reveals yet another mode of gonial-cell proliferation in both male and female phases. In the active testis, spermatogonial cells border the testicular acini, into which the developing male gametes are packed closely. During sex reversal the oogonial cells are in an ovarian anlagen outside the testicular region and separated from it by a thick basement membrane. It is not clear whether the spermatogonial cells from the acini migrate through the epithelial barrier, turning into oogonial cells, or whether undifferentiated gonial cells already in the testis give rise to oogonial cells. That the spermatogonial cells in the testicular acini are capable of giving rise to oogonial cells is evidenced by the precocious differentiation of several spermatogonial cells into oocytes in the testicular acini. This recalls a condition found in the non-functional hermaphroditic crayfish, *Pontastacus leptodactylus leptodactylus*, where the spermatogonial cells in testicular acini give rise to oocytes when the androgenic glands are very small (Payen, 1973). In in-

FIGURE 11. Magnification of area shown in Figure 10 in the regions of cellular disintegration. Note the concentration of pycnotic nuclei (arrows) without cell boundary. Bar = 25 μm.

FIGURE 12. Transverse section through the anterior region of the hermaphroditie ovary of an intersexual (CL 28 mm) showing the row of vitellogenic oocytes (VO) on the dorsolateral region. Note the invasion of follicle cells (FC) digesting the yolk. Bar = 25 μm.

FIGURE 13. Showing the delamination of the follicle cells (FC) into the vitellogenic oocytes (VO). Bar = 10 μm.

FIGURE 14. Transverse section through the middle region of a hermaphroditic ovary of an intersexual (CL = 28 mm) to show the hyperactive somatic mesodermal cells (MC). TC = Testicular acini; MT = metacercaria; PV = Previtellogenic oocytes. Bar = 150 μm.

FIGURE 15. Transverse section through the oviduct of an intersexual (CL 29 mm) to show that it is in an undifferentiated condition. OD = Oviduct. Bar = 150 μm.

FIGURE 16. Transverse section through the hermaphroditic ovary of an intersexual (CL 29 mm) in the middle region. The testicular acini is filled with mucus (M). A few previtellogenic oocytes (PV) are also present. Bar = 100 μm.

FIGURE 17. The posterior-most region of the gonad of a large intersexual (CL 28 mm) indicates the presence of thick mucous coating (M). It also shows the vas deferens (VD) with sperm mass substance inside it. PV = Previtellogenic oocytes. Bar = 25 μm.

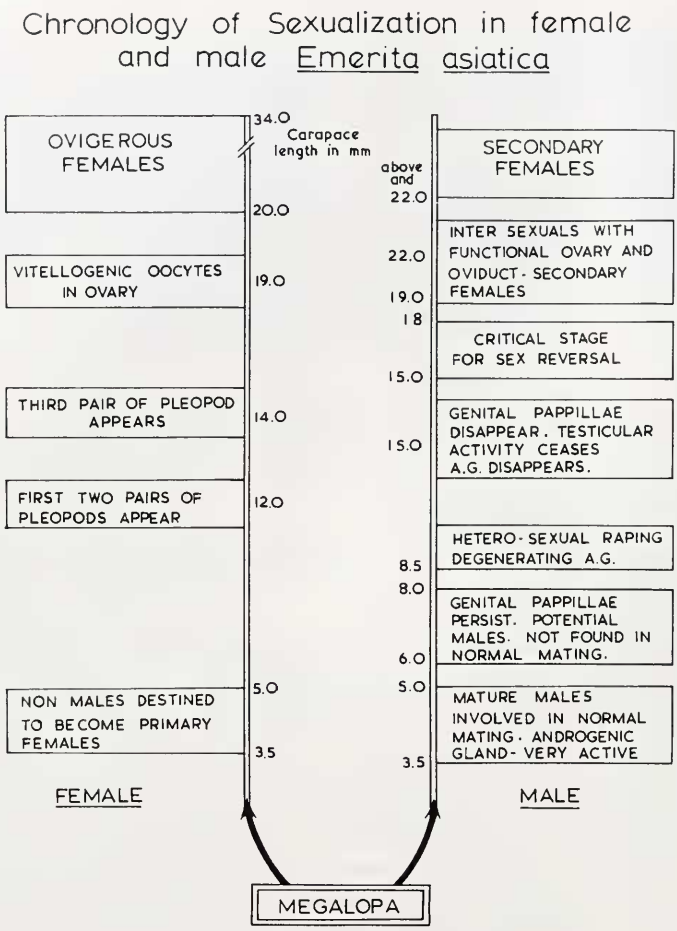

FIGURE 18.

complete sex reversals in *E. asiatica*, a separate ovary is not formed but oocytes differentiate in the dorsolateral periphery of the inactive testis. Alternatively, therefore, it is possible that male and female gonocytes germinate in a common zone in the dorsal surface of the testis all along its length, giving rise to testicular acini early in development. In *P. borealis* and *L. seticaudata*, oogenesis does proceed to previtellogenesis during the male phase, while the active spermatogonia move out from both sides of the ventrally placed germinal zone to surround the ovarian core (Charniaux-Cotton, 1975a).

In *P. borealis*, Allen (1959) has also shown that all prawns showing external male characters have an ovarian germinal strand. Such an intersex condition in gonadial activity has not been observed in the present study on *E. asiatica*. In fact, the ovarian transformation of the testis does not occur soon after the stoppage of spermatogonial activity. Instead, there is a period of quiescence of the gonocytes. Again, a pair of thin walled oviducts with distinct gonopores are present during the male phase in *P. platyceros*. But in *E. asiatica* the secondary female sexual characters do not appear until after the formation of the ovarian anlagen. The

oviducts are differentiated only in intersexuals 19 mm CL and larger. Interestingly, in incomplete intersexuals of 28–29 mm CL the oviduct remains incompletely differentiated, resulting in failure of ovulation.

An important feature of sex reversal in *E. asiatica* is the change in the functional morphology of the somatic mesodermal cells of the gonad. During the active male phase these somatic mesodermal cells are small, and confine themselves to the interspaces between the testicular acini. Once the testis loses its function, the mesodermal cells become hyperactive. Such hyperactivity of the mesodermal cells in the testis during periods of sexual inactivity has also been shown in *P. leptodactylus leptodactylus* (Amato and Payen, 1978). During sex reversal, following the formation of separate ovarian anlagen, the ovarian structure contains typical follicle cells that have either migrated from the testicular region or differentiated from a pre-follicular mesodermic tissue of the gonad. These cells characteristically attach themselves to the vitellogenic oocytes and are flattened on the oocyte surface, probably mediating uptake of vitellogenic proteins from the hemolymph (Charniaux-Cotton, 1975b). In the partly transformed hermaphroditic females of *E. asiatica*, however, the mesodermic cells are numerous, and they produce a thick mucous coat around the posterior testicular portion of the gonad. In addition, the lumina of the testicular acini are filled with such secretions. These substances are probably secreted by the mesodermic cells of the testes. It is of interest to note here that the ovarian follicle cells of a hermit crab, *Clibanarius clibanarius*, are also rich in acid mucopolysaccharide substances (Varadarajan and Subramoniam, 1980).

In incomplete transformation of the gonad, the follicle cells around the vitellogenic oocytes occupying the anterior region of the gonad assume the function of enzymatic digestion of the yolk materials by invading the ooplasm. Follicle cells participating in the oosorptive process have been observed in several crustacean species (Carayon, 1941; Baffoni, 1962).

All this implies an important role for mesodermal cells in the sex reversal of *E. asiatica*. It is tempting to suggest a strong influence of androgenic gland hormone on the activity of these cells as indicated by its apparent disappearance in males above 15 mm CL, possibly ushering in sex reversal.

It is generally accepted that inversion of the sexual phenotype is influenced by epigamous factors exerted during growth (Gallien, 1959). In malacostracan crustaceans the hermaphroditic potentialities are governed by the androgenic gland hormone (Charniaux-Cotton, 1965a, for references). The sequential disappearance of primary and secondary male characters during the changeover phase and the concomitant assumption of female characters strongly suggest similarities with protandric hermaphroditic natantians such as *P. borealis* and *L. seticaudata* with regard to androgenic gland control of sexual differentiation. A high androgenic gland activity when the neotenous males are reproductively active, and the degeneration of the androgenic gland during the gradual disappearance of male secondary sexual characters and stoppage of spermatogonial activity in larger males, clearly suggest that a fall in circulating androgenic gland hormone may be responsible for these changes in *E. asiatica*. Extirpation and grafting experiments of androgenic gland in *L. seticaudata* have yielded similar results (Charniaux-Cotton, 1959, and Berrear-Bonnenfant, 1963).

Touir (1973) brought forward new data that in hermaphroditic natantians the circulating androgenic gland hormone determines the appearance, growth, and maintenance of male external sex characters, whereas in gonochoristic decapods the gland is only capable of provoking the appearance of these characters, and is

not needed to maintain them. More recently, Touir (1977a, b, c) has provided experimental evidence that in the hermaphroditic prawn *L. seticaudata*, this hormone is not indispensable for spermatogenesis, but that it regulates intensity of spermatogenic activity as a result of its mitogenic action on the gonia. A factor from the brain is said to maintain the male genital apparatus. Another factor from the protocerebrum is suggested to be responsible for the maintenance of the androgenic gland, and the absence of this factor causes the disappearance of the gland in *L. seticaudata*. In the light of these observations it may be suggested that the sex reversal in *E. asiatica* is brought about by the disappearance of the above two protocerebral neurosecretory factors.

The incomplete transformation of sex in some large crabs may corroborate this bihormonal influence of sex reversal. In these animals, the neurosecretory substance controlling the spermatogonial activity may disappear completely, so that spermatogonial activity stops. At the same time, the autodifferentiation of oocytes in the anterior half of the paired testis may support the existence of gonadal territoriality in responding to the androgenic gland hormone, as proposed by Legrand (1964). The implication is that a low titer of the hormone prevents the oocytes from reaching previtellogenesis, by inhibiting the folliculogenesis in the posterior testicular territory. On the other hand, the anterior ovarian region, free from the gland's influence, may allow oocytes to undergo vitellogenesis but because of the incomplete oviductal differentiation, oosorption occurs with the help of follicle cells. The retention of the vas deferens in these crabs suggests that the gland has not completely disappeared, thus preventing the complete transformation of sex. Experimental evidence along these lines is highly desirable.

Protandric hermaphroditism is not uncommon among Malacostraca. However, this record of the phenomenon in *E. asiatica* is significant and points to the high probability of sex reversal in such species of *Emerita* where the males attain precocious sexual maturity in the post-larval stage.

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